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STUDY OF MONKEY, APE, AND HUMAN MORPHOLOGY AND PHYSIOLOGY
RELATING TO STRENGTH AND ENDURANCE

PHASE VIII

FACTORS IN THE SUPERIORITY OF CHIMPANZEE OVER HUMAN STRENGTH

William E. Edwards

July 1965

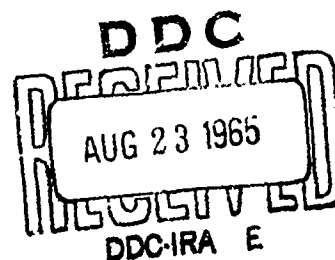DDC

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FOREWORD

This is the eighth in a series of nine papers concerned with the Study of Monkey, Ape, and Human Morphology and Physiology Relating to Strength and Endurance. This study was conducted in part in 1963 under Contract AF 29(600)-3466, Project 6892, Task 689201, monitored by Major James E. Cook, Veterinary Services Division, ARV. Certain of the studies were conducted by the author over an interval of several years, part during his tenure as a National Science Foundation Science Faculty fellow at the University of Chicago, 1959-1961.

The author wishes to acknowledge the cooperation of Lt Col Hamilton H. Blackshear, Major Clyde H. Kratochvil, Major James E. Cook and Major Robert H. Edwards, all of the 6571st romedical Research Laboratory, for their help in the preparation of this paper.

Publication of this report does not constitute Air Force approval of the report's findings or conclusions. It is published only for the exchange and stimulation of ideas.

C.H. KRATOCHVIL
Major, USAF
Commander

ABSTRACT

Detailed consideration and testing of hypotheses against available data
indicate that the marked two-to-one superiority of chimpanzee over
human upper extremity strength per unit of body-weight is apparently
due to a combination in the chimpanzee of relatively larger upper ex-
tremities, higher proportions of contractile material, smaller average
body-size, muscle origins and insertions farther from joints, obliquity
of muscle fibers, greater capillary density and glycogen storage in
muscles, and greater frequency and ease of innervating a higher per-
centage of motor end-plates, but not to different physico-chemical
processes of muscular contraction and not, among the subjects tested,
significantly to difference in exercise, although somewhat differential
response to equivalent exercise is likely.

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FACTORS IN THE SUPERIORITY OF CHIMPANZEE OVER HUMAN STRENGTH

1. INTRODUCTION

The marked superiority of the chimpanzee in muscular strength relative to man is of interest theoretically and in practical applications.

In the context of pure science, an understanding of the factors operating to produce these appreciable differences -- whether by physico-chemical processes or by simple mechanics -- for one set of tested muscles, such as flexors of the forearm, would probably make it possible to estimate very closely the strength of other muscle sets by quickly testing the other sets of muscles only in humans and making gross anatomical, histological, and/or chemical comparative measurements and tests required. The determination of approximate strength differences for various sets of muscles which were the subject of special theoretical or practical concern could almost certainly be achieved far more economically than would be the case if subjects had to be trained and tested in the experimental laboratory for each set. This economic advantage would be maintained even if the predicted strength values for one or two sets of muscles were also checked by experimental strength testing -- as would be advisable to provide additional assurance that only the factors determined for the first set were significantly operative for other sets of muscles. Considered more broadly, an understanding of the causative factors in the strength differences between the chimpanzee and man would also likely provide the key to a comparable interpretation of other interspecies and even interphyla contrasts in strength, endurance, and associated functions. Interpretation of how such differences developed through evolutionary history would also have equivalent theoretical significance.

In applied science terms, knowledge of the nature and extent of strength differences between the chimpanzee and man would be very useful to most experimentation involving the use of chimpanzees as analogs of man, for differences in strength apparently constitute the most marked functional distinction between the two species other than those of higher mental processes. Thus wherever sets of muscles differ appreciably in strength and in their manner of moving the parts of the body they affect, consideration of these differences must be made in designing all testing apparatus in order to secure equivalent performance. Strength and endurance variables must also be known for proper extrapolation of test results to man, as in acceleration studies[1] and long-term performance in space capsules.

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[1] Marked differences in muscle strength would quite surely be associated with equivalent differences in associated tissue distortion and traumatic effects in response to a given acceleration for a given interval, however brief.

The first step in the determination of the factors producing superiority in chimpanzee strength is the formulation of hypothetical factors which might account for all or part of these differences, followed by a preliminary testing of the hypotheses through readily available data and principles. The formulation and preliminary testing of such hypothetical factors constitute both the major purpose and the scope of this paper.

2. STRENGTH OF CHIMPANZEES RELATIVE TO HUMANS

A. General Considerations

As here employed, strength will be limited to a physical, mechanical usage, equivalent to force. In organisms, strength refers to contractile force, the sole function of muscles. Strength is often mistakenly confused with some related phenomena: work, which is the action of force through a distance; power, which is the rate of doing work; and endurance, which refers to relative ability to maintain a given power through time.

Absolute strength refers either to the contractile force developed by a muscle fiber along its main axis (absolute fiber strength) or, as a step removed from this most basic application of the term strength, to the entire contractile force of the muscle along its main axis, that is, upon the tendons (absolute muscle strength). It might be observed that the axes of muscle fibers may be very different from the axis of the entire muscle, so the muscle's absolute strength is not simply the summation of that of its constituent fibers. Third, internal leverage strength is the strength of the muscle acting upon the body itself, with greater or lesser effect depending upon its leverage and its angle to the main axis of the segment of the body resisting motion. Fourth, external leverage strength is that force applicable to an object outside the body.

External leverage strength is the most readily and frequently measured. Internal leverage strength is difficult to determine at all precisely (Edwards, 1963a, p. 2). Absolute muscle strength measurements would be even more useful in theoretical analyses, but are almost impossible to determine in living subjects, with the exception of amputees trained to operate individual cineplastic-tunneled muscles; with such subjects, Ralston et al.(1949) determined values of 2.38, 1.31, and 1.63 kg./cm.[2] for the biceps brachii, triceps, and pectoralis major. The strength of excised solitary muscles may also be determined in vitro; the resulting values will be higher than in normal voluntary contractions, but the relative values should be fairly valid.

Determination of the strength of individual muscles is therefore especially difficult. But there is a simpler method of determining the approximate relative strength of individual muscles -- the method formulated by the writer several years ago and employed to a limited extent in 1961 in studies of the squirrel monkey (1965b; 1965c). The fleshy portion of the

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muscle must have tendons at both ends able to withstand the maximum
contractile force of the organ. Such maximum force is normally reduced in
nature by rapid motion of the body segment; hence the grasshopper's extensor
tendons are fractured at the "knees" when its legs are restrained (Hoyle,
1958, p. 31). Tendon strength will usually be only slightly in excess of
the maximum force normally exerted by the muscle during its lifetime, for
excessive strength would represent in the evolution of the muscle an anti-
adaptive oversufficiency.

It might be anticipated, therefore, that the strength of the muscle
would be proportionate to the cross-sectional area of its tendon just below
its origin or above its insertion. But tendon, generally stronger than bone
in resisting force per unit of area, varies fairly widely in composition and
thus in strength. In the chimpanzee studied by the writer (1965d; 1965e),
tendon cross-sectional area varied from approximately 0.85 per cent of
maximum cross-sectional muscle belly area in latissimus dorsi to 3.2 per
cent in biceps brachii to 28.1 per cent in palmaris longus. In these muscles,
most of the fascicles closely paralleled each other and the axis of con-
traction of the muscle. Latissimus dorsi is not too representative because
its muscle fibers vary in their alignment by as much as 55 degrees, and the
contractile force is at least slightly reduced by its proportionately large
friction-producing surface. At the other extreme, the ratio is unduly high
in palmaris longus due to the somewhat bipennate form of its fleshy portion
and to its probable incipiently vestigial nature (Edwards, 1965e). In
addition, the optimum diameter of the tendon of insertion may greatly exceed
that dictated by tensile strength requirements alone, for this very super-
ficial tendon is unusually susceptible to mechanical injury.

Because of the variable composition and strength of tendon, to apply
the present method, it is necessary to test the tendon strength directly.
In the method developed by the writer, a strong nylon cord is wrapped about
the tendon near its termination and this cord is gradually loaded along the
axis of normal muscle pull; the force at which the tendon breaks is recorded.

For some time, the writer thought that the loading method of estimating
muscle strength was possibly his own innovation, but he then learned that
Borelli (1685) used a similar method almost three centuries ago; since the
time of Borelli, the method has doubtless been discovered by a number of
other investigators as well.

The cross-sectional area of bone -- or, more precisely, its mass per
unit of length -- should also provide at least a rough indication of muscle
strength, but the strength required in most cases is that needed to resist
a large number of muscles operating in a wide variety of directions on
bones of markedly varying length, form, and composition; the characteris-
tics of a given bone are determined by other stress-resisting needs as well.

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B. Results of Strength Testing

Anecdotal observations indicate that, at least in times of stress, chimpanzees are much stronger than humans under normal conditions, but such observations are inadequate for an evaluation of relative strength under comparable extent of motivation or stress. Some thirty-seven criteria are requisite for adequate strength testing of chimpanzees (Edwards, 1963a).

Bauman (1923; 1926) secured very high strength scores on one adult male and one adult female chimpanzee, with an apparent ratio of superiority to humans per unit of body-weight of approximately 2:1 to 3:1 for two-handed pulls by the entire body on a loop or rod handle with the legs flexed and braced. The ratio for the similarly positioned but very different one-handed pull was approximately 4:1.

Finch (1943), in more sophisticated experiments, procured two-handed (per unit of body-weight) ratios for pulling on a handleless rope averaging 1.33:1 for adult male and 0.91:1 for adult female chimpanzees when compared with adult male humans (calculated by the present writer).

Although the ratios obtained by Bauman and Finch are very inconsistent, the contrasting results are not necessarily due to any fundamental error in measuring or recording, and all reports are likely valid. Reconciliation can apparently be adequately achieved through consideration of likely differences in the subjects' condition and the marked differences in methodology. Especially significant are the effects of facilitation of grasp (handles) and the contrasting motivations employed. Even in the "deliberate" scores utilized by the present writer in computing the ratios for "Suzette" and "Boma," the maximum second level of strength was likely exceeded, while apparently the eight chimpanzees of Finch were inadequately motivated to reach that level (see Edwards, 1963a).

It was thus very tentatively concluded by the present writer that -- for those not very precisely identifiable muscles involved -- under comparable conditions chimpanzees are very roughly two times as strong as humans in the two-handed pulls when a handle is provided and disproportionately stronger in the one-handed pulls noted. But neither Bauman, Finch, nor any other investigator has satisfied more than a few of the thirty-seven criteria formulated by the writer (Edwards, 1963a) and shown to be requisite for an adequate program of strength testing of non-human species.

With consideration of the inadequacies in previous studies, in 1961 the writer was employed as a consultant by the Aeromedical Research Laboratory of Holloman Air Force Base to conduct a program of training and testing the strength of chimpanzees and humans. In this research program, it was possible to satisfy almost all of the criteria required for adequate testing. This testing revealed that, per unit of body-weight, the pulling strength of chimpanzees is approximately twice that of humans tested under comparable conditions. The testing apparatus and the training employed

were designed to measure only the strength of the flexors of the forearm; further experimentation will be required before elevation-retraction of the scapula and extension of the brachium can with certainty be excluded from the force values recorded. In any event, it can be concluded at the present time that, contrary to the findings of Finch, chimpanzees are markedly superior to humans in at least the one set, or group of related sets, of voluntary muscles tested (Edwards, 1965g).

3. HYPOTHETICAL FACTORS IN THE STRENGTH DIFFERENCES

A. General Considerations

"A walking animal is an articulated girder structure," with the skeleton representing the compression members and the muscles and ligaments constituting the tension members (Ritchie, 1928, p. 2; for more extensive discussions, see Thompson, 1942).

One or occasionally more than one fulcrum may intervene between the proximal and distal tendons of a muscle. The fulcrum may be intermediate between the tendinous attachment (force) to the moving member and the center of gravity (resistance) of the moving member (a first order lever system), as in the action of the triceps in extending the antebrachium. Or the tendon -- force -- may be intermediate (a third order lever), as in flexion of the forearm by the biceps. Theoretically, the center of gravity of the moving member -- resistance -- may also be intermediate (a second order lever), but because motion would be so relatively restricted by this last arrangement, it occurs in the human body only in a few contestable or infrequently occurring cases, such as plantar flexion of the feet raising the body on tiptoe if the ball of the foot is regarded as the fulcrum. A little further consideration of the mechanics involved reveals that internal leverage strength is inversely proportionate to the maximum translocation of the body segment moved; so in evolution greater strength or mobility is almost always achieved primarily at the cost of the lessening of the counterpart (mobility or internal leverage strength, respectively), except where the increased mobility is accompanied by proportionately larger or more "efficient" muscles.

The detailed structure of muscles and the physico-chemical processes involved in their contraction have already been considered at length by the present writer (1963a) and many others, so no further general discussion of this area will be given here.

B. Effect of Exercise

The effect of muscular exercise will be the first hypothetical factor considered because it potentially affects many of the other factors.

Two Chinese porters may be able to lift on a litter an American prima-
tologist -- so obese as to equal their combined body-weights -- and then
trot along for hours at a time at a pace much faster than the primatologist
could have maintained on foot without any burden. The investigator, tending
not only to take himself for granted but also to employ himself as the
standard upon which to measure all comparable phenomena, may marvel at the
remarkable strength, endurance, and, to a lesser degree, the slightness of
body-build of the porters. What he may not consider is that, along with
much of the modern world's population, he is the atypical representative of
the human species. Likewise, a chimpanzee may seem extremely strong in
comparison with the average laboratory worker but not with that worker's
much stronger Cro-Magnon forebears of a thousand generations past. On mid-
winter days these ancestors might walk or run as much as 30 miles in their
search for game before killing a mammoth; then, to avoid forcing their
wives and children to leave the relative comfort of their cave, each might
carry 150 pounds of meat 10 miles back to the encampment before resting.
Furthermore, some of the muscles of the chimpanzee, especially those of the
upper extremities, are generally used far more than comparable muscles in
man -- even ancestral or recent but non-Western man.

In a review of the "chronic effects of exercise," Steinhaus (1933)
gives the increase in muscle mass as probably the best recognized result
of long-time muscular exertion. The increase is due entirely to true
hypertrophy of existing muscle cells, not to any increase in number of
cells, in length of fibers, or number of nuclei; only the sarcoplasm is
increased (p. 105).

The number of capillaries functioning in the active muscle of a trained
athlete shows an increase over resting muscle of at least 400%, while the
size of each capillary increases approximately 100% (Krogh, 1929, p. 182).
The resulting capillary bed facilitates the interchange of oxygen, food-
stuffs, and waste products, causing still more capillaries to become
operative. Hence oxygen can diffuse more readily to the tissues; with
local accumulations of heat and lactic acid, oxygen dissociates more easily
from the hemoglobin of the red blood corpuscles. Thorndike (1962) and his
co-workers at the Harvard Fatigue Laboratory no longer regard lactic acid
exclusively as a toxin but as a natural outcome of exertion. "Owing to
this change in skeletal muscles during exercise, the amount of oxygen
utilized per unit of arterial blood can be greatly increased and these
tissues may consume per unit weight as much as fifty times the oxygen they
consume at rest" (Thorndike, 1962, pp. 56-57).

In the trained athlete red cells and plasma proteins may show a 10
per cent increase during a football game, while the leukocyte count might
rise to 200-300 per cent of normal. This is probably due to the diffusion
of lactic acid into the blood from the tissues; water and electrolytes move
into the tissues to equalize osmotic pressure; loss of water from the blood
increases the proportion of blood cells. In 1933 Steinhaus wrote: "There
is no agreement as to whether a period of training produces a lasting
change in the number of red corpuscles. The current belief that training

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induces a gradual increase in the per cent of hemoglobin, the total mass of corpuscles, and the total volume of blood, rests on but meagre experimental data" (p. 118). The data accumulate, but agreement does not come, perhaps because of the failure to isolate the variables.

C. Different Absolute or Relative Dimensions

The length of muscles does not in itself increase the force exertable unless the fibers do not have the usual form or alignment parallel to the main axis of the muscle (see section G below). But muscle absolutely or relatively larger in cross-sectional area will, all else being equal, manifest proportionately greater strength, absolutely or relatively. Therefore, if the arms of the chimpanzee were not only proportionately longer but also heavier, the chimpanzee would through this factor be expected to be stronger than the human, body-weight being equal.

D. Different Proportions of Contractile Material

If the fleshy portion of the human muscle had higher components of non-contractile material, such as connective tissue, fatty deposits, or blood vessels, it would, all else being equal, be expected to be proportionately weaker than the comparable chimpanzee muscle.

E. Different Body-Size

By principles of geometrical similitude, strength is proportionate to the square of a given dimension, all else being equivalent -- not to body-weight, which is proportionate to the cube of a given dimension (Edwards, 1963a). Thus if chimpanzee strength scores are compared per unit of body-weight with those of larger humans, the chimpanzee should by this factor manifest slightly greater strength. For example, despite proportionately thinner arms and legs, gibbons can brachiate much longer and faster and can walk erect more readily than their larger and, if appearances were valid, relatively stronger ape cousins (Edwards, 1963h). As but one non-primatological example, in this way can also be readily explained the otherwise remarkable strength of the grasshopper; each of the grasshopper's hind-leg extensor muscles, weighing only 2 per cent of the body-weight, "exerts the astonishing power of some 20,000 grams per gram of its own weight." Such great strength is due in small part to the obliquity of the muscle fibers (see section G below) but, although not recognized by the major investigator of this phenomenon (Hoyle, 1958), is ascribable mainly to the fact that the grasshopper is small relative to most terrestrial vertebrates.

F. Different Locations of Insertions or Origins Relative to Joints

As the mechanical analysis in section A above indicates, if all characteristics of a pair of compared muscles (with relatively distinct origins) are equal except the point of insertion, and if this point is

twice as far down the long-bone in the chimpanzee as in man, the muscle
will be able to exert almost twice as much force in the ape. Fairly obvi-
ously, doubling of both origin and insertion distances doubles the effec-
tive force while leaving the mobility range unaffected.

Somewhat similarly, the effective muscular force may be increased
through angular change by displacement of the origin farther from a joint
which is between the origin and the insertion. But in a large proportion
of cases, the major axis of the muscle is nearly parallel to the surface
of the bone on which it arises and over which it might migrate through
sufficient evolutionary time, so there would be no significant improvement
in mechanical advantage when the muscle of more distant origin is extended
in this manner. However, upon contraction, the main axis of the muscle
with the more distant origin becomes slightly to markedly more perpendi-
cular to the moving segment.[2]

Generally more important as a determinant of origin position, the
range of mobility of the affected body segment is approximately propor-
tionate to the total muscle belly length, which in most cases is most
readily increased by migration of the origin.

Likely a comprehensive search of the literature in comparative
anatomy or muscular physiology would result in the discovery of several
discussions of the precise effects of migrations in points of origin and
insertion. But since such analyses are not presently available to him,
the writer has calculated trigonometrically the effects of varying the
distance from the joint (fulcrum) to the insertion and to the origin. The
most frequent case in vertebrates -- that of a single joint intermediate
between the two muscle attachments, generally associated with a third
order or rarely (as in the action of the brachioradialis of the potto, to
be discussed) a second order lever system -- was chosen for the analyses,
with fiber alignment parallel to the muscle axis and doubling of all lever-
arm lengths (more precisely, joint-to-attachment distances, for the usage
of "lever-arm" will here be limited to the moving segment bearing the in-
sertion), as simplifying assumptions. The results of these calculations
are summarized in Table 1.

Several generalizations may be derived from the table, which nec-
essarily assumes minute points of origin and insertion that in actuality
usually comprise relatively broad areas of attachment, thus somewhat
complicating the mechanical analysis of the situation. In muscles of
approximately equivalent joint-to-origin and joint-to-insertion distances,

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[2]A much more significant gain in a higher origin would accrue if the
belly were likewise extended, because a smaller proportionate contraction --
and thus a smaller relative loss of maximum force -- would then be required
for a given angular movement.

Table 1

Effect of Variation in Position of Parallel Muscle Origin and Insertion

	Change in Proportionate Perpendicular Component by Change in Angle between Lever-Arm and Force of Lever-Arm	Change in Mechancial Advantage	Change in Internal Leverage Strength (Force-Arm), Constant Muscle Tension	Change in Angular Mobility Range
I. Doubling Lever-Arm (Joint to Insertion)				
180 – c. 90* Condition A	Slightly decreased	Doubled	Slightly less than doubled	Moderately to appreciably decreased (from good to fair)
c. 80	Slightly increased to slightly decreased	Doubled	Approximately doubled	
180 – c. 90 Condition B	Decreased to approximately two-thirds	Doubled	Increased approximately one-third	Markedly increased (from poor)
c. 80	Decreased to approximately five-eighths	Doubled	Increased approximately one-fourth	
180 – c. 90 Condition C	Decreased to slightly more than half	Doubled	Slightly increased	Slightly increased (from good)
c. 80	Approximately halved	Doubled	Approximately unchanged	
II. Doubling Joint-to-Origin Distance				
180 – c. 90 Condition A	Slightly increased	Unchanged	Slightly increased	Slightly increased (from good)
c. 80	Slightly increased to slightly decreased	Unchanged	Approximately unchanged	
180 – c. 90 Condition B	Increased approximately one-third	Unchanged	Increased approximately one-third	Markedly increased (from poor)
c. 80	Increased approximately one-fourth	Unchanged	Increased approximately one-fourth	
180 – c. 90 Condition C	Almost doubled	Unchanged	Slightly less than doubled	Moderately to appreciably decreased (from good)
c. 80	Approximately doubled	Unchanged	Approximately doubled	

*Angle in degrees formed by the intersection of the main axes of the fixed and movable body segments

Condition A Lever-arm (joint to insertion) much less than joint-to-origin distance
Condition B Lever-arm roughly equal to joint-to-origin distance
Condition C Lever-arm much greater than joint-to-origin distance

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doubling of either distance increases the internal leverage strength 23 to 35 per cent at most angles, and moderately increases the angular range of mobility. But even with parallel fascicle alignment, mobility is extremely limited if the joint is roughly equidistant from the two points of tendon attachment; if, with muscle relaxation, the axes of the movable and fixed members are almost in the same straight line, the two members cannot by contraction of this muscle be brought into closer apposition than approximately 60 degrees. Furthermore, large or superficial muscles, and especially those both large and superficial, would have to be able to raise proportionately large ridges above the surface of the skin, which would in turn require adaptation of adjacent structures and necessitate greater susceptibility to mechanical injury.

So for most muscles it is highly advantageous to have the distance from the joint to the attachments very unequal, with the muscle body nearly paralleling (and in a large proportion of cases closely adjacent to) the underlying bone upon which the more distant attachment is made. As Table 1 shows, when the lever-arm is very short, doubling its length effects an almost proportionate increase in effective muscle force.[3] But if the lever-arm is much longer than the joint-to-origin distance, almost proportionately greater strength results from an increase in the distance to the origin. As a seeming paradox, then, equal distances from joints to attachments are generally very disadvantageous, but if these distances are highly unequal, partial equalization improves strength with little loss of mobility.

If two muscles are dimensionally and structurally identical, the nearer the insertion is to the joint the proportionately smaller is the loss in maximum exertable absolute muscle force due to shortening of the fascicles for a given angular movement -- the counterpart of the advantage of longer

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[3]Actually, the force exerted on the insertion is less than twice as much because of the more acute angle at which the force is acting -- assuming that the joint is between the muscle's origin and insertion -- and because of the slightly smaller perpendicular component resulting at the point of insertion. This perpendicular component is the "force-arm," the resultant at a right angle to the axis of the resisting lever-arm in the plane through this arm and the main axis of the muscle; the muscle axis is the line of force, except in cases in which the tendon of insertion bends around a ligament or bone pulley. Only if both the distance of the origin and of the insertion from the joint were doubled would the effective force acting on the body segment be doubled, as noted previously. Although the internal leverage strength increase due to distalward extension of the insertion while the origin remains unchanged is less than the proportionate increase in the lever-arm because of the more acute angle of the muscle, in terms of external leverage strength this angular reduction is in many cases more than counterbalanced by the reduction in the percentage of resistance constituted by the movable body segment -- assuming the mass of that segment remains approximately constant.

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muscle bellies, as previously observed. But if two muscles have the same angular mobility ranges and are otherwise closely similar except for different insertion distances, the one with the more distant insertion will generally achieve its maximum internal and external leverage strength at greater angular movement upon contraction.

Consideration of muscle physiology and mechanics shows that in general greater strength is achieved at the expense of lessened mobility. But if the distances from the joint to the attachments are very unequal, an increase in the longer distance results in a slight theoretical increase in mobility -- although in such cases maximum mobility was probably attained before the change. More frequently significant, the longer muscle belly will undergo less decline in force as the mobility limit upon contraction is approached (see footnote 2).

At least a small vector in the resultant optimum of muscle length and location of attachments ensues from the fact that more distantly attaching muscles with dimensionally constant fleshy portions require greater tendon mass -- and in many cases additional spatial problems associated with movement relative to contiguous organs.

All factors considered, it may be concluded that for parallel muscles the optimum distances from the joint to the origin and to the insertion are generally markedly unequal but not extreme in such inequality.

In addition to the maximum force, the distribution of maximum exertable force at different amounts of movement, and the mobility range of muscles, other basic functional aspects of muscles which are influential as additional vectors determining the compromise resultant form include speed -- as exemplified by adaptations of the leg of the horse (Hildebrand, 1960) -- and endurance. Another factor, retarding the evolutionary rapidity of migration of muscle attachments in all vertebrates, is the competition for limited space for bony attachments in certain areas.

In some cases, either the origin or insertion may be relatively stable because of the lesser significance of the muscle as compared with those surrounding it. For example, the primate coracobrachialis may vary more in origin than in insertion the writer would suggest, because the general area of origin of adjacent brachialis is fixed by its function, and expansion of the origin of brachialis would not be appreciably useful. Thus coracobrachialis, perhaps largely through the lack of very strong demand for the area by contiguous muscles, occupies its insertion area fairly uniformly, although apparently not at a point or area very precisely fixed by function.

If, because of competing needs, an attachment cannot feasibly migrate farther from its location very near the joint (but see section G) to achieve

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greater strength,[4] the need may be satisfied by a change from parallel to
oblique (unipennate or bipennate), or from oblique to more oblique, fiber
alignment, although such an arrangement is not quite as efficient mechani-
cally because of the additional tendon required, and although the maximum
strength of the pennate muscle is much more variable at different degrees of
contraction (see below). Such a process has occurred in the wrists of chim-
panzees and humans, where minimization of spatial requirements has high
selective value for mechanical reasons and where bipennate muscles generally
restrict their fleshy contractile portions to the forearm, well above the
wrist and hand where these muscles operate with relatively great force and
complexity. Hominoid hands also exemplify the fact that leverage does not
always undergo change in proportion to the migration of attachments because
the mobility of the fleshy portion of a muscle and especially of its tendons
is often limited by the fixed position of other organs or the difficulties
which would arise from excessive plasticity of the dermis; for example, the
deep flexors of the digits have gained relatively little in leverage from
the migration of their origins up the forearm (Straus, 1942, p. 312), for
they are bound by ligaments and other tissues to fairly constant positions
within the carpal, metacarpal, and phalangeal segments.

It might be anticipated that since a significant gain in mechanical
advantage is potentially derivable through the migration of insertions more
frequently than of origins, insertions should manifest greater interspecific
variability. Yet -- despite some partial exceptions, such as teres minor --
in the primates, as in all major groups of vertebrates, insertions show
decidedly greater stability. The explanation for this phenomenon is that the
points of insertion are generally much more closely associated with function,
so their feasible range of migration tends to be much more limited; for
example, major changes in the areas of origin of flexor pollicis longus may
affect minor alterations in the extent, force, and angle of movement, but a
shift in the insertion to the palmar aponeurosis would result in entirely
different functions.

As but one of hundreds of potential primatological exemplifications
of one or more of the foregoing principles, the potto (Perodicticus) of West
Africa has long been noted to have a remarkable brachioradialis, inserting
on the radial styloid process and extending in its origin on the humerus
from the lateral epicondylar ridge to as high as the surgical neck (Hill,
1953, p. 184).

Presumably, no detailed analysis of this unusual feature has previously
been offered, so the writer will at this time attempt such an interpretation,
which should prove illustrative of underlying principles. The insertion is
obviously related to this massive muscle's functions of supinating and, more

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[4]Because of the requirements of geometrical similitude, greater strength
constitutes a progressively more pressing need in large animals -- and the
evolutionary trend in most animal and especially mammalian groups has been
toward larger size.

importantly, flexing the forearm. If this muscle had the same proportionate size as the relatively slim presumed long head of brachioradialis of the squirrel monkey, which -- as recently discovered (Edwards, 1965b and 1965c) -- has equivalent points of attachment, very little augmentation of strength would result from the unusually high origin. But in the potto the fore-limb is permanently bent at the elbow; the potto's massive brachioradialis is thus able to produce a much greater degree of flexion of the antebrachium (although total mobility remains quite low) and, because of the less acute angle, is relatively powerful even when the forearm is extended as fully as structure permits. In this way, some of the disadvantages noted for muscles with attachments equidistant from the joint are missing.

Interestingly, the origin of brachioradialis extends almost as high on the humerus of the Madagascar indri lemurs, in which the muscle manifests approximately the same massiveness of development and is associated with similar permanent flexion at the elbow, obviously for the same fundamental advantage pertaining to mobility and leverage.

Exceptional conditions almost seem to demand explanation, however; in this case, the very unusual form of brachioradialis in the potto and the indri should be considered. First, unlike the varied movements required of almost all higher primates in locomotion and the manipulation of food, there is much less emphasis on mobility or agility in these quite typically quadrupedal lower primates. Yet the excessive development of brachioradialis, and to a lesser extent the limited degree of antebrachial mobility, are not found in equivalent degree among the other lower primates. So if it is granted that selective pressures for maintenance of high mobility are less in the lower primates than in monkeys, apes, and humans, there must still be sought compensating mechanical-functional advantages of the brachioradialis of the potto and indri which do not occur in the form and/or function of the majority of lower primates and which provide compensation for the reduced mobility.

The potto is generally quite slow-moving relative to most strepsirhines, which suggests a further reduction, compared with most other lower primates, in selective pressure for maintained mobility. Furthermore, it is nocturnal, protecting itself in the daytime primarily by hiding. If attacked, it curls up and presents its nuchal region -- the most vulnerable area of most primates, but in the potto protected by thick pelage and unique dorsal spinous processes from the last cervical and first two thoracic vertebrae which protrude from the skin (Hill, 1953, p. 176). The attacked potto clings "by hands and feet with so powerful a grip that removal of the animal involves the application of sufficient violence to cause mutilation of its extremities" (Hill, 1953, p. 190).

The foregoing data explain only in part the case of the indri, however. Like other lower primates, it can better afford lessened mobility than the higher primates, but although sluggish it is apparently faster than the potto

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and places less reliance on passive defense.[5] It might be suggested that the similarity is due to closeness of relationship, with descent of the indri from a potto-like ancestor; but the relationship within the primates of the potto and the indri is very distant indeed. However, a satisfactory factor to which at least much of the hypertrophy of the brachioradialis can be ascribed is the relatively large body-size of the indri, the largest extant lower primate, with much larger relatives rendered extinct quite surely only upon the relatively recent arrival of man in Madagascar (Hill, 1953, p. 628; Edwards, 1960a). The muscle's massiveness and relative distance between origin and insertion and the permanent partial flexure of the antebrachium are thus largely if not entirely ascribable to the requirements of geometrical similitude that larger animals must have disproportionately larger muscles and/or improved leverage for these muscles for their equivalent function, and that function will tend to be maintained almost equivalently if it is crucial to survival.

Some indirect confirmation of this last interpretation is provided by the apes, in which the requirements of mobility prevent the origin of the brachioradialis from moving far up the humerus. The much more moderate mechanical demands associated with geometrical similitude in the smallest ape, the gibbon (Hylobates), have permitted the insertion to migrate up to the middle of the radial shaft (Hill, 1957, p. 32), while remaining relatively distal in origin (Straus, 1941, p. 26).

In previous discussions in this paper, little consideration has been given to variability -- and thus adjustability -- in muscle belly dimensions. All else being equivalent, the force a muscle can exert is proportionate to its average cross-sectional area. Thus it might seem that the relationship between the relative massiveness of a muscle and its attachment distances from the joint are precisely inversely related for constancy of function, and are therefore capable of very arbitrary variation in relative dimensions. Such an analysis implicitly ignores bone and joint diameters, however. Despite such cases as the elbows of the potto and indri, long-bones articulated to one another in the limbs of land vertebrates generally extend end-to-end in essentially the same straight line upon extension of the body segment. Muscles attached to two such bones of infinitesimal diameter would upon extension exert infinitesimal flexing or hyperextending force; thus internal leverage strength is under such conditions proportionate to the diameter of the bones and the cross-sectional area of the muscle. So muscles would tend to be very thick and short and to insert only in the joint area. On the other hand, there is insufficient space near the joints for all parallel muscles to manifest optimum thickness and areas of insertion. Also, it should be considered that since bones and joints have thickness, mobility would be excessively limited if the muscles were too short; for the thicker the joint, the greater is the absolute contraction of the muscle necessary to produce a given angular displacement, everything else being equal.

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[5]Apparently the only very effective predator of the indri before man's recent arrival was the civet cat.

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Since the force-arm tending to produce angular movement in one of two
body segments, each containing long-bones articulating end-to-end and ex-
tended in the same straight line, is approximately proportionate to the
diameter of the bones, a major factor tending to increase bone dimensions is
recognizable. The foregoing consideration thus largely explains why a mouse
has a proportiontely heavier skeleton than equivalent compression strength
requires relative to a human, as well as proportionately larger bones rela-
tive to their weight (Edwards, 1960b). The advantages of better leverage
also helps to account for the development of various types of bony protuber-
ances, including ridges -- both for origins and especially for insertions --
to enable points of muscle attachment, and therefore application of force,
to be farther removed from the axis of the joint. The principle here consi-
dered applies especially to enlargement of bones at the joints, a phenomenon
thus seen not merely to reflect a need for greater structural strength in
areas of greater stress, as many have suggested.

G. Non-Parallelism of Muscle Fascicles to Tendons

All else being equivalent, the total absolute fascicle strength (or, to
employ its component elements as the basic unit, absolute fiber strength) is
proportionate to the product of the average cross-sectional area of the aver-
age fascicle and the total number of fascicles. Therefore, the absolute
strength of a muscle with the simplest parallel alignment of all fascicles to
the tendon of insertion can be increased without altering its general size or
form. This requires only an increase in the number of fascicles by their
shortening and turning obliquely to the main axis of the muscle (which is
normally essentially identical to the axis of the insertion tendon), as in
unipennate, bipennate, and multipennate muscles, so-called because the fas-
cicles converge to one or both sides of the tendon like the plumes of a
feather.

The writer feels that a quantitative analysis of the factors involved
should clarify and exemplify any generalizations derived from such consider-
ations. In each of the three following examples to be analyzed for this
purpose, the proximal end of the muscle is at or just beyond the distal tip
of a broad bone, distal to which are two articulating, parallel, 50-cm.
long-bones with mid-lines 12 cm. apart; the second and third bones articu-
late in turn with a fourth, most distal bone, upon which the muscle inserts.
The first example studied will be that of a simple, parallel muscle (condi-
tion A) -- which is very roughly represented by gastrocnemius in the
chimpanzee and man -- originating from the transversely extending distal end
of the broad bone and extending fleshily with constant width (12 cm.) and
thickness (1 cm.) to its transformation to tendon 30 cm. from the origin.
The unipennate second condition (B) represents conversion to shorter fasci-
cles (24 cm.), arising along the mid-line of the medial of the two parallel
long-bones for 30 cm. and inserting at an angle of 30 degrees upon a tendon
extending along the opposite side of the muscle. Fascia and tendon attaching
the lateral-border tendon to the lateral long-bone and to the fourth bone
upon which the tendon inserts strongly pull the lateral-border tendon
laterally and distally and effectively serve to hold the lateral tendon in
place and to permit slight movement only proximally-distally upon sufficient

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muscular contraction and relaxation -- this somewhat unrealistic arrangement
has the function of simplifying mechanical analysis. The bipennate third
condition (C) is provided by a muscle like the second but converted to short-
er fascicles (12 cm.), each as in the unipennate muscle not originating prox-
imally from the transverse area of bone but from along the mid-lines of both
parallel long-bones and inserting into a median tendon extending the length
of the fleshy portions; the fascicles again form an angle of 30 degrees with
the median tendon and thus with main axis of the muscle and its tendon of
insertion -- thereby approximating the condition of soleus of the chimpanzee
and man.

In all three conditions, the muscle is composed of large bundles 1.0
cm.^{2} in cross-sectional area, which are in turn composed of 1.0 mm.^{2} fasci-
cles. Employing a fairly representative value of 3,000 gm./cm.^{2} (Haxton,
1944; Ralston et al., 1949), the 1,200 fascicles in the 12 bundles of the
parallel muscle can exert a maximum force of 36,000 gm. when at 100 to 125
per cent of equilibrium length (Høncke, 1947, p. 195). The muscle can
contract to 50 per cent of its equilibrium length, providing mobility of
15 cm. at the point of insertion. The minute volumetric change upon contrac-
tion is not significant.

In condition B, the unipennate muscle also has 360 cc. of fleshy muscles
and extends appreciably farther distally, with 15 bundles yielding an abso-
lute fiber force of 45,000 gm. but, because of the obliquity of the fibers to
the tendon of insertion, the absolute muscle strength is 38,970 gm., only
slightly more than that of the parallel muscle. If the medial and lateral
margins were kept parallel and constantly 12 cm. apart, the proximal movement
of the lateral tendon (and therefore of the insertion) would be 20.78 cm.;
but at near-maximum contraction, the direction of force would be almost
perpendicular to the lateral tendon, so the longitudinal component of force
would be almost infinitesimal. Thus it seems more realistic to assume con-
stancy of muscle fiber obliquity to the lateral tendons, in which case there
is only a normal diminishing of force with fiber shortening; the mobility is
then 10.39 cm., only 69.3 per cent as great as that of the parallel muscle.
Even at the optimum angle of obliquity of 45 degrees (see below), the maxi-
mum pull is increased only slightly to 45,000 gm. and the mobility is
reduced to only 6 cm., assuming constant obliquity. In view of the fore-
going calculations and the difficulties encountered by the muscle upon
contraction in maintaining tautness of the insertion tendon border without
excessive lateral movement, the reason for the relative rareness of almost
purely unipennate muscles in nature can be perceived.

On the other hand, the 360 cc. bipennate muscle of condition C is com-
posed of a total of 30 bundles (3,000 fascicles), each with a length of 12
cm.: the total absolute fiber strength is 90,000 gm. and, when adjusted for
the non-parallelism of the fascicles to the tendon, 77,940 gm., more than
twice the exertable force of the same-sized parallel muscle. Maximum mobil-
ity (total muscle contractility) is reduced to 10.39 cm. in theory, but at
that degree of contraction (to 50 per cent of fascicle length at equilibrium),
the fibers would all be perpendicular to the tendon, so there would be no
absolute muscle force. The fibers might retain some 60 per cent (although

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probably appreciably less) of their maximum force upon contracting to a length of 6.928 cm., 57.7 per cent of the original (equilibrium) length. At that degree of contraction (6.928 cm. displacement of the insertion), the angle of fiber obliquity to the central tendon would be 60 degrees and the absolute muscle strength would be 27,000 gm. The bipennate muscle strength is approximately equal to that of the comparable parallel muscle, which would have undergone fiber contraction to 76.9 per cent of initial length to accomplish the same movement at the muscle insertion and might at that length retain an equivalent strength of 27,000 gm. (75 per cent of its maximum force at equilibrium length). The effective strength provided by the bipennate muscle thus exceeds or approximately equals that of the parallel muscle over a range of 6.928 cm., 46.2 per cent of the total range of mobility of the parallel muscle; in this one case exactly reciprocal of that mobility percentage, the force exertable at equilibrium is 216.4 per cent that of the parallel muscle, and the bipennate muscle can still provide additional movement after the contraction here considered (to 57.7 per cent of its original length). It might thus seem, from the advantages indicated, that bipennate muscles represent the most efficient (as well as most complex) of the three forms, and would thus be expected to be universal among animals (but see below).

To complete the foregoing analysis, the work performed by the parallel and bipennate muscles here considered will be computed. When the fascicles of the parallel muscle contract 0.1 per cent at maximum load, 36,000 gm. are lifted .03 cm., for total work of 1080 cm.-gm. Each fascicle of the bipennate muscle contracts equivalently .012 cm., producing an apparent displacement of .01039 cm. in 77,940 gm., for 809.8 cm.-gm. of work, 75 per cent as much work as that produced by the parallel muscle (total work thus appears to be proportionate to the square of the absolute muscle strength divided by the total absolute fiber strength). But the insertion end of each fascicle moves away from the muscle insertion (and therefore "pulls" the muscle insertion with it the same distance) not simply toward the origin of the fascicle, as might seem to be the case, but is held in the mid-line by the simultaneous contraction of the fascicle on the opposite side, causing an additional displacement. In this case, when the fascicles shorten .012 cm. to 11.988 cm., the length-wise distance down the mid-line, from a point at the level of a fascicle's origin to its insertion, is reduced from 10.3923 to 10.3784 cm., producing a total displacement of .01388 cm. and total work of 1080 (more precisely 1081.8) cm.-gm., identical to that of the parallel muscle. Thus in comparing parallel with bipennate muscles of the same given length, the same equilibrium length, and the same muscle mass, the products of maximum exertable force and displacement produced by a given percentage of equilibrium length of fiber contraction always equal one another.

Continuing with the writer's original (although not necessarily innovating) analysis, all geometrically similar muscles of whatever form, all else equivalent but size, require identical proportions of tendon -- a characteristic of constancy rather infrequently encountered in the application of geometrical similitude. Since the tensile stress on a bipennate muscle's median tendon is distally cumulative, this tendon may be extremely slender at the proximal (origin) end, but at the distal (insertion) end of the belly it must approximate its maximum cross-sectional area.

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The already evident advantages of bipennate muscles can now be considered more explicitly. Most of the advantages of the bipennate form accrue from its generally greater strength. All else being equal, parallel muscles are weaker and thus require insertions and/or origins farther from the joint. But when the limb, for example, is extended nearly straight -- and strength at the time of straightening of the body portion is often very crucial -- migration of an origin or insertion which is nearer the joint to a greater distance adds very little to the leverage, as explained previously, despite the expense of lessened mobility. Bipennate muscles may more than counterbalance a faster rate of decline of absolute muscle strength upon contraction (see below) through relative constancy of the force-arm -- the perpendicular distance from the axis of rotation to the line of force -- even when fully extended, as discussed previously, since such stronger muscles can be attached nearer the joints. Thus in many cases bipennateness enables muscles to manifest greater constancy of both internal and external leverage strength over the range of movement of a body segment. Bipennate muscles are also advantageous for moving short body segments, such as the digits of many vertebrates, because insertions can closely approximate the joints. Finally, bipennateness is especially advantageous where, for greater strength needs, increase in the length of muscles is more feasible than increase in cross-sectional area, as in the antebrachium of all larger primates, such as chimpanzees and humans. In this last case, it is evident that a bipennate muscle functions in large measure as a substitute for a shorter and more massive parallel muscle.

The reason that bipennate muscles do not constitute the predominate form should also be considered. Most important, generally, is the factor of mobility, which, as evident in the preceding analyses, undergoes reduction inversely with the degree of increase in exertable force of the bipennate organs. Even though increased strength enables bipennate muscles to be inserted nearer joints, net mobility is in many cases decreased. It should also be considered that, in accord with principles of geometrical similitude, smaller animals rarely have difficulty in achieving adequate muscular strength without sacrificing mobility. Furthermore, although absolute fiber force decreases as muscle fibers of all muscle types contract, in bipennate muscles the angle of obliquity also increases (very rapidly if initally large) and thus greatly accelerates the decline in absolute muscle strength upon contraction. This accelerated decline in strength is so rapid that in many cases the relative constancy of internal leverage strength is lost in the later stages of bipennate muscle contraction and concomitant body portion movement, with little if any external leverage strength in the final phases of movement. Also, to maintain the same total mass in bipennate as in parallel muscles entails fairly appreciable losses in the ability to perform work because of the requisite conversion of fascicles into tendon. The median tendon requires otherwise unnecessary material, while the distal portion of the tendon of insertion must be appreciably thicker, assuming the muscle-tension-resisting strength of the tendons is the limiting factor. In the hypothetical contrast of parallel and bipennate muscles considered above, the distal tendon must theoretically more than double in mass to resist increased stresses, although the greater linear extent of the fleshy portions makes possible some shortening and thereby less than doubling of this distal tendon. Finally, as previously noted, areas of attachment away from the joint

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might theoretically receive greater competition for space, but because of the advantages of bipennate muscles in many cases and the more limited areas available near the joints, it seems probable that competition for attachment-space is generally much greater for such joint attachments, at least in larger animals, as seems confirmed by the concentration of insertions near joints. The area of bony attachment also needs to be larger for stronger bipennate muscles, thus adding further difficulty for bipennateness.

Relatively longer bipennate muscles require proportionately larger median tendons and heavier distal tendons. So it might seem that shorter bipennate muscles are superior. On the other hand, a bipennate muscle, with an angle of obliquity of 30 degrees and with a fleshy portion which is as wide as it is long, is slightly weaker than a parallel muscle of the same fleshy dimensions -- although oddly, as a compensating gain, the bipennate muscle (with tendons shorter than the parallel muscle's to counterbalance the greater belly length) actually manifests the greater mobility range. When the equilibrium angle is 45 degrees, both the force and the maximum mobility of a roughly square bipennate muscle belly are identical to those of a parallel muscle of equal size, but the bipennate organ has appreciably less strength compared with the parallel muscle when maximum contraction is approached. This seeming exception to the principle of constancy of maximum work (average force multiplied by distance) which a muscle of given fleshy volume can perform is due to the inability of fascicles at 45 degrees at equilibrium to contract fully. In view also of the added burden of additional tendon, the reason bipennate muscles tend to be relatively long -- with increasing strength in approximately direct proportion to length -- is readily recognized. The writer would in fact suggest that very short bipennate muscles found in any animal are in the process of evolutionary reduction or even conversion to vestigial structures. But since the proportion of tendon increases with length, there is a limit to the feasible length of such obliquely aligned structures, with an optimum length perhaps 4 to 8 times as great as the breadth.

The optimum distance of bipennate insertions from joints should be analyzed further than indicated in previous discussion. Since a relatively long bipennate muscle with a fairly large angle of obliquity manifests great strength but small mobility, insertion far from the joint would result in a very small angular range of mobility and a rapid loss of strength (maximum force) as the body segment moves. Furthermore, a distant insertion generally adds relatively little to the force-arm when the segment is fully extended. Therefore, bipennate insertions tend with rare exceptions to concentrate very near joints, providing a greater need for resistance of stress and thus another factor promoting bony expansion at and near joints.

The effect of varied angles of alignment is also worthy of consideration. Absolute fiber strength varies precisely inversely with fiber length for a given muscle belly mass, but in bipennate muscles the absolute muscle strength is reduced by the factor of the cosine of the angle of obliquity of the fibers to the main axis of the muscle (which the central tendon generally closely coincides with or at least parallels). Calculations by the writer show that the angle producing maximum strength in a bipennate muscle is 45 degrees at equilibrium. Computation reveals perfect symmetry in maximum force at equal

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divergences above and below 45 degrees at equilibrium, with the increase
in the component of force parallel to the tendon for angles less than 45
degrees precisely counterbalancing the increased number of fascicles as
the angle is increased equally in excess of 45 degrees.

The factor of mobility also enters into a determination of the opti-
mum fascicle alignment angle. At the representative proportion of length
to breadth of 6, if a parallel muscle belly and individual fascicles of a
bipennate muscle can contract to 50 per cent of their equilibrium lengths,
maximum contractility is less than one-twelfth (approximately 8 per cent)
of the total belly length when the equilibrium angle is 45 degrees. But
at an equilibrium angle of 18.4 degrees, at which the longitudinal and trans-
verse distances traversed by a single fascicle have a ratio of 3:1 instead
of the previous 1:1 at 45 degrees, the contractility of the fleshy por-
tion of a muscle with a length-to-breadth ratio of 6 is 14.8 per cent,
and at an equilibrium angle of 9.5 per cent the belly will contract 23.3
per cent of its length along either side. In the last example maximum
strength is only 197 per cent that of a comparable parallel muscle, how-
ever, while at 18.4 degrees it is 360 per cent and at 45 degrees it is
fully 600 per cent (without consideration of loss due to a larger tendon).

It may be concluded from the previous examples and calculations that
the optimum bipennate angle at equilibrium for cases with strength all-
important and movement negligible is 45 degrees; but in actuality strength
over a range of movement is always significant, and marked reduction of
the total range of mobility is rarely a negligible factor. The optimum
angle of bipennate obliquity is thus a compromise between a greater angle
(up to 45 degree) -- for shorter fibers and therefore for greater abso-
lute fiber strength -- and a smaller angle -- for a greater proportionate
component parallel with the muscle's main axis, for greater mobility, and
for a much slower decline in absolute fiber force as the fibers shorten
and the angle of obliquity increases. Despite some anatomical illustra-
tions to the contrary, and with the possible exception of an unusual
form of muscle distortion at rest (Fulton, 1950, p. 123), bipennate
structures should always manifest alignments appreciably less than 45
degrees except when approaching their maximum range of contraction.
Theoretical computations indicate that the angle of obliquity of bipen-
nate muscles at equilibrium should show a mean value approximating 20
degrees. Likewise, bipennate muscles are correlated with insertion
close to joints and the need for great force, as in plantar flexion of
the human foot by soleus (aided by gastrocnemius, which manifests much
less obliquity, however, largely because it extends across two joints
and must retain greater motility).

Completing the writer's analysis of the mechanical factors involved
in muscle size, form, and alignment, the factors determining the frequency
in nature of muscles combining parallel with oblique alignments should be
considered. At least two features shared by parallel and bipennate mus-
cles and having some relevance to a mechanical analysis of muscle form
and function might be noted. First, all requirements of strength at
various positions and the frequency of the various positions of the body

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segments involved enter into the determination of the optimum relative contraction of the muscles at the body segment's full extension; but generally the optimum is that body segments comparable to primate limbs must frequently be slightly flexed (both in the case of parallel and of bipennate muscles, but especially of parallel muscles), with flexor muscles at approximate equilibrium at the slightly flexed position and with slight stretching of flexors by contraction of extensors required for full extension of the body segments. Second, is previously alluded to, for both parallel and bipennate muscles, reduction of absolute muscle force upon the muscle's contraction -- in bipennate muscles both by shortening fascicles and by increasing angles of obliquity -- is generally more than compensated for during the early phase of movement by increased perpendicularity of the muscle axis to the body segment being moved.

In many cases of combined parallel and pennate muscles, one determinant is the availability of only a single suitable longtitudinal or oblique strip of origin area. But in many cases equally significant, it seems probable to the writer, is the advantage in division of an elongated muscle into fairly equal halves by a median tendon, with nearly parallel fascicles arising proximally from a transverse area of origin, and with many of the fascicles on one side proceeding almost longitudinally and quite distally before inserting upon the median tendon. On the other side of the tendon a gradual transition proximally to distally from almost parallel to progressively more oblique fascicles may occur, with angles typically as great as 25 to 30 degrees at equilibrium if a suitable longitudinal strip of origin is available. For many muscles, such an arrangement constitutes the optimum compromise (or in this case combination) of maximal strength and maximal mobility, for such a muscle, with a length-breadth ratio of 6, may have a maximum strength of two to three times that of a comparable parallel muscle, and yet may achieve motility almost equal to that of a parallel muscle, albeit with only about half the parallel muscle's strength after a relatively small amount of contraction has occurred. The reason for the frequency of combination parallel-pennate muscles, with a wide variation on the pennate side in the angles of obliquity -- and a regularity in the pattern of angular change -- seems fairly evident.

Tappen and Wickstrom (1961) developed a measure of muscular force which involved dividing the weight of the isolated muscle by the mean length of its fascicles as a substitute for calculating the functional (physiological) cross-section. Commenting on their "force ratio," they say that "the anatomical and functional cross-sections are virtually identical in the human sartorius. The force ratio of one segment of the sartorius, 0.162, is equivalent to 109 mm.^{2}, the cross-sectional area secured by tracing and measuring with a planimeter" (p. 441).

The present writer's contention that the force ratio would be most generally meaningful as a measure of absolute muscle strength if multiplied by the cosine of the weighted average of the angles of alignment was largely anticipated in 1944 by Haxton, who applied the correction to the gastrocnemius, which he reported formed an angle of 10.5 degrees

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between its fibers and the tendon of insertion, and to the soleus, with an angle of obliquity of 25 degrees. Contrary to Tappen and Wickstrom, and a fallacy among strength investigators that goes back at least a century to Weber, the "reduced physiological cross-section" of Haxton's specimens bore a consistent ratio to the anatomical cross-section -- of 1.31:1, although certain theoretical arrangements of fascicles or fibers could reduce the significance of cross-sections.[6]

H. More Glycogen Storage; Slimmer Fibers; Greater Capillary Density

The factors affecting endurance are at least somewhat significant to virtually any testing of strength itself, since it is impossible entirely to separate the dynamic from the static aspects of muscle force. Such factors include the quantity of glycogen stored in the muscle to be utilized when the muscle is stimulated to rapid contraction. Considering the chimpanzee's frequently dynamic personality and frantic activity level, it does not seem unlikely that its muscles might contain greater reserves of power.

Superior muscle metabolism might result at any point in the chain of chemical reactions (the "Cori cycle") governing strenuous exercise and recovery. In a rapid anaerobic breakdown of muscle glycogen, energy in quantity is instantly available. Lactic acid is formed as a by-product. There is a great increase in blood flow to the active muscle and, since almost no oxygen is stored in the muscle itself, it draws oxygen from the blood as soon as it reaches the muscle tissues. If there is efficient circulation and an abundant supply of oxygen, therefore, the lactic acid combines with it and is reconverted to glycogen. If the activity is very intense, however, the lactic acid accumulates faster than it can be oxidized. The muscle becomes fatigued, deprived of oxygen, and depleted of its glycogen store. The accumulated lactic acid diffuses into the blood stream and is carried to the liver, where is turns into liver glycogen (which can be reduced to blood sugar as needed). The heightened acidity of the blood, as a result of the influx of lactic acid, serves as a signal to the respiratory center in the brain and initiates forced breathing, which continues long after the exercise ceases, until the "oxygen debt" is paid off. This recovery phase of muscular activity involves the oxidation of about one-fifth of the accumulated lactic acid remaining, and provides the energy by which the other four-fifths is resynthesized into glycogen.

Lactic acid also figures in the resynthesis of the organic phosphates, which have been omitted here for simplicity, but which serve as another source of energy in the reversible reactions of muscle contractions.

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[6] Another theoretical possibility for increasing muscle strength, again at the expense of mobility, is by shortening the fascicles or fibers, increasing their number and cross-sectional area by "dovetailing." Perhaps this does not occur in nature because of the very long tendinous extensions that such fascicles would need.

Various anatomical differences might give a species an important advantage in muscle metabolism. Slimmer fibers and a greater concentration of smaller capillaries are two features that would facilitate both the clearance and utilization of lactic acid and more rapid osmosis of supplies and waste products, notably oxygen and carbon dioxide. Significant differences might be found to exist in such characteristics if chimpanzees and humans should be subjected to critical comparisons.

I. Different Physico-Chemical Processes of Muscle Function

The description in the foregoing section is, of course, a rather standard, modern textbook version of muscle physiology (e.g., Morgan, 1955; Youmans, 1957; Langley and Cheraskin, 1958). Some of the concepts have changed markedly even in the last generation; 30 years ago, for example, lactic acid was regarded as a waste product that poisoned the muscles, as referred to previously. As the human mind can visualize alternative explanations of phenomena, so is evolution theory and the record rich with variation. It is at least theoretically possible that the chimpanzee -- or his ancestors after divergence from the common man-chimpanzee ancestor -- evolved superior physico-chemical processes of muscle action. Alternatively, it is conceivable that the common ancestor developed superior processes which were lost in subsequent human evolution.

J. Different Ease and Frequency of Motor Unit Innervation

Available studies indicate that, in the vast majority of humans, maximum effort involves the "firing" of perhaps half of the voluntary muscle fibers. Apparently because of different firing thresholds for individual fibers (Scheer, 1953, p. 298), stronger innervation stimulus results in greater muscular contraction. Chimpanzees may simply be more responsive than humans, with stronger (or at any rate more effective) innervation than humans under non-emergency conditions.

4. EVALUATION OF THE SUGGESTED HYPOTHETICAL FACTORS

A. General Considerations

The emphasis chosen for this paper is the development of as broad a range of hypothetical factors pertinent to the observed superiority of chimpanzee over human strength as possible -- not the thorough testing of such hypotheses. In any case, presently available data do not admit of definitive evaluation. For the foregoing reasons, the evaluations which follow will be very cursory and incomplete.

B. Effect of Exercise

Jungle-dwelling chimpanzees have, at least for the upper extremities, much more exercise than even migratory hunting humans inhabiting the same area, and the apes should certainly manifest relative hypertrophic effects on strength when compared with average Western humans, non-sedentary only on rare occasions. However, all of the chimpanzees

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studied by Bauman (1923; 1926), Finch (1943), and the writer (1965g) had spent years (and in many cases virtually their entire lives) in rather closely confining cages. Their average quantity of general physical exercise was almost certainly less than that of the average human tested in these studies, and among the chimpanzees and humans tested by the writer, the chimpanzees experienced appreciably less exercise than that of most of the human subjects, whom the chimpanzees outscored by a ratio of approximately 2:1. Careful observation of the chimpanzees in their cages suggests that the chimpanzees in the writer's study may possibly have exceeded the humans to a slight degree in the average exercise of the musculature tested, that of the upper extremities; but even that very limited advantage seems doubtful. It may thus be concluded that the chimpanzee superiority in strength here considered cannot be ascribed to any significant degree to hypertrophy through greater exercise.

It seems at least moderately likely, however, that in response to higher selective pressures[7] the chimpanzee has evolved the reaction of greater muscular hypertrophy to a given quantity of exercise stimulus. This last hypothesis may seem only semantic, but further consideration reveals its non-fallaciousness.

C. Different Absolute and Relative Dimensions

First, it is clear that both the brachial and antebrachial segments of the upper extremities tested are relatively longer in the chimpanzee, both relative to trunk height and lower limb length (Schultz, 1933). Although length is not significant to the almost perfectly parallel brachial flexors (as well as to latissimus dorsi and teres major), the primary sources of the strength recorded, they are significant to the bipennate and possibly force-contributing infraspinatus and teres minor -- as well as to most of the antebrachial musculature (see below).

The relative external transverse dimensions are also moderately larger in the chimpanzee, as comparison of the brachial and antebrachial girths listed in the writer's recent study (1965g), for example, make evident.

Comparison of skin-fold measures (Hunsdon, 1958) for chimpanzees and humans, checked briefly by the writer in 1961, and the smaller percentage of fatty deposits in the chimpanzee, repeatedly observed on dissection by various investigators and confirmed by the writer (1965d; 1965e), reveal a further advantage of the simian over man. Consequently, it seems clear that although cross-sectional data on the musculature of humans (Weber, 1849) are almost as sparse as that on the chimpanzee, chimpanzee muscles are fairly decidedly superior in relative cross-sectional area, which is proportionate to strength in parallel muscles, all other factors equal. This conclusion receives some corroboration from consideration by any experienced human anatomist of the cross-sectional drawings and measurements provided by the writer (1965d; 1965e).

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[7]Or perhaps more likely a decline may have occurred in man in this respect in response to lower selective pressures (see below).

D. Different Proportions of Contractile Material

Throughout the animal kingdom, interspecific, intraspecific, and even intraindividual comparisons reveal extreme variability in connective tissue, especially in adipose tissue, both within and between muscle bundles (Ritchie, 1928, p. 11; Høncke, 1947, p. 32; Walls, 1960, p. 24). Significantly, this variation also applies to varying concentrations of myofibrils, the basic contractile elements, within each fiber; therefore, two muscles might vary appreciably in exertable strength through differences in the internal composition of their fibers alone.

Since it seems generally agreed that in most respects the muscle action of chimpanzees is at least not quite as precisely controlled, some indirect and only very partial corroboration for the thesis that apes have less non-contractile tissue is found in the fact that "the proportion of connective tissue present is greater in muscles which are capable of finely graded movements" (Walls, 1960, p. 25). More directly, the gross appearance of the chimpanzee muscle dissected by the writer suggests confirmation of the hypothesis, although histological comparisons from various muscles and specimens are needed. At least one very limited study of this type has been made; Hopf (1934) found that in microscopic appearance chimpanzee masseters differ markedly from those of man and other mammals, such as the hedgehog, a primitive insectivore.

E. Different Body-Size

Since the average body-size of the chimpanzees studied by Bauman, Finch, and the writer -- especially those tested by the writer -- averaged less than that of the human subjects, geometrical similitude results in favoring the chimpanzee in strength scores per unit of body-weight. This resultant of conformity with geometrical similitude is a fairly appreciable factor for the smaller species; all else being equivalent, a 60-pound individual should outscore a 160-pound one 38.7 per cent (Edwards, 1965g). On the other hand, general observational data on chimpanzees seem in accord with the results of extensive comparative strength testing of immature and adult humans; even after adjustment for larger body-size, mature individuals are fairly markedly stronger than pre-adolescents or early-adolescents, the age category of four of the writer's five chimpanzee subjects. In comparing a representative 120-pound adult male chimpanzee with a typical 160-pound human male, consideration of the effect of geometrical similitude on general body-size results in an expectation of a 10.1 per cent superiority of the chimpanzee per pound of body weight -- not too appreciable, but accounting for part of the observed differences.

F. Different Locations of Insertions or Origins Relative to Joints

The writer's recent study of chimpanzee anatomy reveals that better leverage in muscle attachments provides at least a portion of the strength superiority.

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For example, the insertion of biceps in the writer's specimen was
from 34 to 53 mm. below the proximal end of the radius (length 283 mm.),
with the axis of rotation some 6 mm. above the end of the radius. The
length of the lever-arm beyond the axis of rotation is thus 41-60 mm.,
which is 14.5 to 21.2 per cent of the projection of the radius beyond
the joint. The only comparable data presently available to the writer
are the presumably very precise drawings made from photographs by
Grant (1947, Fig. 56). The dimensions of 8.5 to 19.0 mm., adjusted to
10.5 to 21.0 mm. with a proportionate allowance for the distance from the
axis of rotation to the proximal end of the radius, may be related to the
total radial length of 95 mm. (at the scale shown), for force-arm of radial
length percentages of 11.1 to 22.1. Average percentages, which provide
at least a rough index to relative leverages, are thus 17.9 (ape) and
16.6 (man), providing a leverage advantage of 7.8 per cent to the chim-
panzee. Of course, series (their number depending upon variability) of
both simian and human specimens must be measured for comparisons to be
more than merely indicative.

In the writer's report (1965d) on the thorax and brachium of an
adult female chimpanzee, it was also observed that the areas over which
a number of muscles -- notably pectoralis major and teres minor --
inserted are decidedly greater than in man; extending farther from the
joint, they also provide superior leverage for the ape.

Some origins may also extend significantly farther from the joint;
since the major axis of a muscle arising farther from a joint forms a
larger acute angle with the segment moved, an increased perpendicular
component results. In the writer's chimpanzee specimen, the long head of
triceps extended 40 per cent of the distance along the axillary border
from the glenoid cavity to the inferior angle; Grant (1947, Fig. 26) does
not show the extent of this origin in man too clearly, but indicates an
approximate extent of only 27 per cent.

Brachioradialis apparently manifests very little difference in
this respect in the two species. The proximal end of its tendinous origin
cannot be precisely defined on the writer's specimen, so the volar border
of the muscle was projected to the humerus, at a point 133 mm. from the
distal end of the 324.5-mm. bone; the origin extends 73 mm. down the hum-
erus. Thus the ape's muscle arises from 59.0 to 81.5 per cent down the
length of the humerus, which is equivalent to a distance from the elbow-
joint of 18.7 to 44.0 per cent of the extension of the radius past the
elbow's axis of rotation (289 mm.). Comparable figures for man, derived
from Grant (1947, Fig. 26), are 61.1 to 85.2 per cent distally down the
humerus (thus proportionately slightly closer to the elbow), and the
distance from the joint is 18.6 to 51.2 per cent of the extension of the
radius beyond the joint (with the apparent inconsistency in the propor-
tions resulting from the relatively longer antebrachium of the chimpan-
zee).

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G. Non-Parallelism of Muscle Fascicles to Tendons

The three forms recently compared anatomically by the present writer seem to provide excellent tests of the principles of muscle form and function developed in a preceding portion of this paper.

Because of its size and the operation of geometrical similitude, the squirrel monkey, one of the smallest of all higher primates, is relatively strong and would not be expected to manifest such adaptations to the need for more strength at the expense of mobility as the development of muscle attachments very distant from their joints and a large proportion of uni-pennate, bipennate, and multipennate muscles. With almost exclusively fusiform or cylindrical muscles with parallel alignment, Saimiri conforms closely to expectation (Edwards, 1965b and 1965c).

Man, a giant and therefore relatively weak primate, manifests many of the adaptive compensations discussed.

Because of its frequent climbing and brachiating mode of locomotion, the chimpanzee, another giant primate, has even greater need than man for structural adaptations of the musculoskeletal system around the pectoral girdle. As might again have been anticipated, many such specializations are evident. For example, although multipennate subscapularis manifests essentially as much obliquity in man as in the chimpanzee, other muscles from the scapula to the crowded proximal end of the humerus near the strength-demanding shoulder-joint[8] -- especially infraspinatus and teres minor -- show more obliquity in the chimpanzee (Edwards, 1965d). Some-what larger angles of obliquity than in man seem also to characterize the chimpanzee antebrachium, with its varied unipennate, bipennate, and parallel-pennate muscles. Pennate muscles derive greater strength from increased fleshy length, so it is not surprising that the upper-extremity-emphasizing chimpanzee displays a marked tendency for extension of fleshy portions of antebrachial musculature as far distally into the margin of the wrist as is at all feasible without appreciable damage to the wrist's mobility, with resultingly much longer muscle bellies than in man. With greater needs, the stronger muscles also seem to secure more concentrated origin from intermuscular septa which are heavier than in man, as well as from the superficial antebrachial fascia, appreciably thicker and more extensive than in man. The customary "price" paid for greater strength when appreciably larger muscle mass is not feasible is reduced mobility. For example, the fact that in man gastrocnemius is not fully taut over the full range of flexion at the knee (Lockhart, 1960, p. 7) may be considered. This limited tautness reflects, as the writer would interpret the phenome-non, the fact that, as a partial compromise for strength needs, some obliquity has developed in gastrocnemius (although much less than in soleus).

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[8]Competition for space is especially great near the shoulder-joint of primates because of their need for extreme mobility as well as strength in that area.

More importantly, the flaccidity of the gastrocnemius over much of the range of rotation seems clearly derived from the fact that, for reduction of mass near the foot, the fleshy-to-tendinous length ratio is low, for such a lowered ratio in near-parallel muscle is associated with very little loss of strength. The gastrocnemius is thus much stronger than a typical parallel-fusiform muscle fleshy over the vast majority of its length, but the increased strength at the most crucial angular range of flexion has been accomplished at the cost of reduced mobility -- or, considering the combined action of all flexing muscles in this area, at the cost of markedly reduced strength over much of the angular range.

The fact that, in contrast with human cadavers, the writer's dissected chimpanzee exhibited marked finger flexion whenever the hand was dorsiflexed -- and the writer has observed the same phenomenon in live apes, as have others --[9] seems most properly assignable to this primary factor of reduced mobility. When the preceding section of the paper in which the potential advantage of dovetailed shorter fascicles or fibers to strength was prepared on purely theoretical grounds, the writer knew of no evidence that fascicles and fibers do not extend the entire length of the bundle (see, for example, Lockhart, 1960, p. 3). But since that time there has been encountered the discussion of Walls (1960, pp. 29-30) that fibers in most muscles do not run the entire length of the bundles. The theoretical strength advantage noted by the writer seems to be corroborated by Walls' statement that muscles with relatively shorter fiber lengths have lessened contractility. Such shortening of fibers rather than fascicles might have the advantage of reducing the need for additional tendon or connective tissue substitute for transmitting the fiber force to the muscle-tendon junction (Walls, 1960, p. 44).

It is therefore possible -- as only detailed histological studies can test -- that the chimpanzee exhibits dovetailing of relatively shorter muscle fibers to a greater extent than does man.

H. More Glycogen Storage; Slimmer Fibers; and Greater Capillary Density

The chimpanzee has more frequent need than man for relatively brief but intensive bursts of energy. On the other hand, the chimpanzee, with frequent eating of calorically less concentrated foods, has less need for food storage. Several studies of dogs have shown augmented stores of glycogen in an exercised leg compared to that in an unexercised leg (Steinhaus, 1933, p. 106). The experimenters have attributed the increased storage to the demands of training, but have consistently noted that the initial rise after a week on a treadmill continued its increase more slowly

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[9]In addition, this characteristic likely serves to strengthen the hand-wrist area and to reduce muscular effort in digital flexion during brachiation.

for some three weeks of additional training and then gradually declined to approximately the value in the unexercised leg, as if the animal had become stabilized to the conditions of training and no longer needed quick sources of energy. No correlations have apparently been found in other animal species, however, between glycogen content of muscles and muscular endurance over long intervals (Wertheimer, 1945). The fairly high interspecific variability in the concentration of glycogen stored in muscular tissue may therefore have relatively little significance anyway.[10] There is also some variation in the maximum lactic acid proportion permitted. Since significant differences between chimpanzees and humans in both characteristics potentially exist, this area seems worthy of investigation.

The writer's theoretical suggestion that slimmer fascicles and fibers should be adaptable to more rapid expenditure of muscular energy finds apparent corroboration in the scale of descending fiber-diameters -- "fish, toads, reptiles, mammals, and birds" (Walls, 1960, p. 26) -- for the same general order of muscular metabolism obtains. More specific confirmation seems at least suggested by the observations of Hopf (1934, pp. 205-206) that the chimpanzee masseter manifests both more varied and generally smaller fibers than those of other mammals, apparently including man. But the advantage of smaller fibers after more than 10 seconds or so of maximal exertion is at least partly counterbalanced by the slight increase in connective and circulatory tissue required.

Interspecific variation in the density of capillaries is appreciable, as is that between individuals, largely due to exercise differences. The redness of muscles is caused by myoglobin; but this seems to be correlated with the relative development of capillaries. It was considered evident that redness of muscle reflected long-sustained effort with less rapid contractility, while "white" muscles were associated with spurts of energy of short duration (Ritchie, 1928, pp. 2-3). The theoretical advantage to endurance of more myoglobin and capillary development but disadvantage to momentary strength by reduction of proportionate contractile tissue seems evident; however, the universal validity of these correlations now seems decidedly in doubt (Walls, 1960, pp. 41-42).

I. Different Physico-Chemical Processes of Muscle Function

Since there is no fundamental difference at present detectable in the physico-chemical processes of muscular contraction in such divergent

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[10]Large quantities of glycogen are stored instead of fat in various parts of the bodies of molluscs, nematodes, and flies (Ritchie, 1928, p. 10). Studying the reserve substances used in flight by Drosophila, Wigglesworth found dense deposits of glycogen in the so-called fat body and suggested that the failure of the flies to use fats to support flight was due to the slow rate of fat metabolism (1949, pp. 150 and 162).

animals as man and frog, temperature considered (Høncke, 1947, p. 196), it seems extremely unlikely that any significant variations in such processes differentiate chimpanzees from their primate relatives.

The inductive approach supports the foregoing conclusion. The possible ways in which muscles might be made to contract are undoubtedly limited. By the time vertebrates developed in the earliest Paleozoic, all such readily available processes had probably been tested through selective trial and error for some billion years of metazoic evolution; it seems improbable that the most suitable processes for fish and amphibia would not also be the most suitable for apes and man. The chimpanzee phylogenetic line may have relatively recently developed some very minor variation adapted to its own idiosyncratic optimal needs. If such minor difference does exist, however, it is far more likely to have developed in man; a mildly deleterious mutation in man might not be removed because of the lower selective pressure, as a result of cultural compensation. Since there has been a geometric progression in the rate of reduction of most selective pressures with the similar progression in the development of culture, it seems probable that any such "defective" variation in muscle function would not be universal among all human races; it would be least likely among Australoids.

J. Different Ease and Frequency of Motor Unit Innervation

As noted in the earlier counterpart of this section, various data indicate that half or less of the muscle units fire at development of maximum force in most humans. That greater power is available as evident in human behavior in emergency situations, under the suggestion of hypnosis, and after certain types of brain damage -- usually those that impair normal inhibition.

The fact that winning Olympic weightlifting scores, each amounting to several hundred pounds, can be predicted within ounces can be explained only by an approach in such performances to the precisely limiting asymptote of all motor units operating simultaneously (Edwards, 1963a).

An interesting series of studies by Ikai and Steinhaus (1961) support the thesis that "the expression of human strength is generally limited by psychologically induced inhibitions" (p. 157). The maximum pull of the forearm flexors during six carefully controlled tests was altered by hypnosis, inhibition-reducing drugs, the surprise of a pistol shot, etc. Before and after pulls show significant changes at levels of confidence from 0.01 to 0.001. Changes in strength ranged, in a predictable direction, from +26.5 to -31 per cent.

The literature of physiotherapy is punctuated throughout this century with reminders that "the most important single element in work output is the will to perform a physiologically maximal effort" (Houtz et al., 1946).

The chimpanzee's exertion of maximum or near-maximum effort readily and frequently, as observed by everyone who has known the species personally (see, for example, Riesen and Kinder, 1952, p. 16), undoubtedly

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indicates stronger and more effective innervation than seen in humans. Physiological factors in general predict only ultimate capacities; but more subtle physiological (and, in such cases as nerves, perhaps morphological) factors can also alter the ease of initiating or intensifying stimulated processes, so the strength differences here considered are likely physiologically based in part. However, it should also be considered that appreciably less than any physiological limits are the actual performances and limited behavior of modern man, influenced by psychological factors.

5. EVOLUTION OF DIFFERENTIATING FACTORS

A. Significance of Evolutionary Considerations

Although its value is little appreciated by many investigators, consideration of evolutionary processes is helpful in understanding all biological phenomena, whether in process of change or the result of past changes. Such a diachronic (historical) understanding can in many cases make possible more accurate final evaluations of the relative significance of the factors affecting a synchronic (at a single point in time) phenomenon if those factors are complex and/or the direction and extent of each factor's "vector" (by analogy with mechanical principles) in determining the resultant phenomenon is not readily analyzable.

In all problems of interpreting organic phenomena, an evolutionary perspective also satisfies purely intellectual purposes, for interpretations of functional phenomena always exist at differing levels, with the diachronic always underlying the immediately "functional" synchronic.

B. Chimpanzee and Human Phylogenetic Divergence in Strength

Even after body-size (and geometrical similitude) and proportionate muscle size are taken into consideration, caged chimpanzees have a fairly marked strength advantage over Western humans -- an advantage which can be little if at all ascribed to environmental factors, such as exercise and nutrition. Evidently there is a residuum of subtle, genetically (including ontogenetically) controlled differences, which must therefore be evolutionary in origin.

Although recent research of the writer indicates that man is most likely not descended from an arboreal ape and the common ancestor must be sought in deposits as early as Eocene in age (Edwards, 1963h), apes probably represent man's closest extant relatives. Thus it is significant to consider whether the differential development of characteristics promoting strength reflects equivalent divergence in opposite directions in this respect from the common ancestor of the chimpanzee and man or whether one phylogenetic line has remained relatively unchanged while the other has diverged. Both general observational data, which seem to indicate strength more nearly equivalent to the chimpanzee in a fairly wide variety of other mammals (body-size considered), and the inductive considerations which follow combine to indicate to the writer that man is an atypical form

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which in this respect has diverged from the relatively conservative, unaltered ape. In evolutionary perspective, then, the fundamental question is not so much "Why is the chimpanzee so strong?" as "Why did humans evolve characteristics reducing maximum strength?"

C. Mutation Pressure

The suggestion of markedly greater relative mutation pressure for deleterious factors reducing strength does not accord with genetic principles. However, despite the high interindividual variability apparently characterizing all species of apes, as demonstrated in a number of studies by Schulz and others, it appears probable to the writer that human populations are in most respects far more variable than those of any other mammalian species, despite contentions to the contrary -- based, the writer believes, on non-representative characteristics. If such extreme variability of Homo relative to other forms is a fact, this phenomenon may reflect a progressive lessening of the optimum uniformity in human phylogeny associated with the advent of culture and the progressive widening of the gap between actual human morphology and physiology (and their distributional ranges) at a given point of time as compared with the culture-determined optimum morphology and physiology at that time. Thus, despite appreciable counteracting "inefficiency" in differentiating the less fit from the more fit for survival in most respects under cultural conditions (constantly accelerating in complexity and influence), the optimum mutation rate probably became higher. Since the general mutation rate is apparently subject to genetic control, it seems likely that a progressively higher mutation rate has developed in man.[11] Therefore, if anti-adaptive genetic factors determining suboptimal strength have developed phylogenetically in man partly through increased mutation pressure, this has fairly surely occurred only as part of a general increase in mutation rates, not through atypically high mutation rates for genes affecting strength and not as "directional" mutations.

D. Maintenance Selection

The assumed extreme variability of man is not necessarily due primarily or even in part to a higher general mutation rate, for such a higher rate in man may be non-existent, as the qualifications in the previous discussion indicate. Such human variability can also be explained through the operation of reduced selective pressures for the vast majority of characteristics under genetic control. Such a reduction has almost surely occurred as a result of the protective aspects of culture, with those features contributing significantly greater general or specific cultural capabilities constituting the sole major exceptions. There is no real doubt, in the writer's opinion,

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[11] If the mutation rate is subject to genetic control, it could have become higher even if the optimum did not change by reduced efficiency in elimination of mutations in the genes controlling the mutation rate, but of course such hypothetical mutations might also have tended predominantly to reduce rather than increase the general mutation rate.

that Western Civilization is associated with drastically reduced maintenance selection for most characteristics, so the precultural dynamic equilibrium between increment and removal of defective mutations has been greatly altered. In fact, any equilibrium under cultural conditions is only a theoretical one, for several millenia would be required even closely to approach it in the genetic composition of a human population. Meanwhile, cultural evolution is causing this equilibrium to change at an accelerating pace; so despite the rapid increase in the proportion of defective genes derived from mutations, the hiatus between the defective level at a given time and the equilibrium level is rapidly broadening. The reduction in maintenance selection characterizing Western Civilization differs only in degree from that in less complex and permissive civilizations, which in turn differ only in degree from more primitive cultures.

It may therefore be concluded that if lessened maintenance selection is the primary historical factor accounting for the reduction in human strength, that reduction should be of lesser magnitude in those races, such as the Australoids and South African Bushmen, which have been affected by very complex culture for a shorter interval of time.

E. Neoteny

It is widely agreed that the evolution of man from a monkey- or ape-like ancestor was accomplished largely through the process of neoteny -- the ontogenetic emphasis on the early stages of growth with relative compression, reduction in emphasis, and in part truncation of the later maturational stages. If it is accepted that this poorly-understood process occurred to a significant degree in human evolution, it likely effected a reduction in adult strength, the associated muscular development of which was linked to more general ontogenetic processes, as was likely the case (but as part of a process of extending the adult growth stages instead) for the excessive growth of antlers in the presently extinct Irish elk.

But reproductive maturity in the axolotl salamander and in man (including "infantile" Negritos) illustrates that reduction of strength through lack of maturation -- although it may have been initiated through neoteny -- would have survived only if it were not selectively too disadvantageous.

In any case, the limited data available on chimpanzees (Edwards, 1963f and 1965g) and humans (various sources) indicate that, body-size considered, human males undergo as much if not a slightly greater increase in relative strength at maturation than do the apes. Despite the complicating influence of cultural-environmental factors in the human situation, especially in the much smaller increase of strength in mature females, it can at least be concluded that available information does not confirm the neoteny hypothesis.

F. Sexual Dimorphism and Sexual Selection

The contrasts between young adult males and females in Western
Civilization in such somatic characteristics as body-weight and quanti-
tative development of musculature (Ritchie, 1928, p. 62) seem to the
writer largely the result of cultural factors, as consideration of
smaller differences in other cultures affirms. Humans thus manifest
less genetically determined sexual dimorphism than any of the great apes,
in which intermale competition for females is based more exclusively upon
physical prowess than among humans, and defense against predators is
primarily a function of males biologically specialized for this purpose.[12]
In consideration of the factors determining the ape and presumably the
common ancestral hominoid (ape and human) sexual dimorphism,[13] it seems
evident that, in dimorphism reduction, males would tend more than females
to shift toward the mean.

During the culture-bearing stages of human evolution, sexual (that
is, reproductive) selection may also have favored weaker (at least, under
non-emergency conditions) than average females, probably through selection
for features correlated with less physical strength than average. Espe-
cially if sexual dimorphism were declining, such selected females would
then have transmitted this relative weakness to male as well as female
offspring. But such a selective tendency seems doubtful; it should in any
case have been fully counterbalanced by sexual-cultural selection for
stronger males, both actively by females and as a concomitant of direct
conflict between rival males, for selection by some females of weaker males
appears to be a recent cultural phenomenon. Interpopulational selection
for groups better defended by stronger males was also of probable signifi-
cance, although culturally developed weapons and techniques acceleratingly
increased their relative importance at the expense of biologically deter-
mined defensive capabilities.

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[12] The active defense of the larger and slower great apes contrasts
with the primary reliance on rapidity of flight in gibbons and siamangs,
which largely for this reason manifest relatively little sexual dimorphism,
like most of their smaller arboreal relatives. Arboreal primates such as
gibbons and marmosets which rely on flight and are also non-promiscuous
and primarily monogamous thus lack most of both major factors favoring
marked sexual dimorphism.

[13] However, a probable near absence of sexual dimorphism in secondary
characteristics in the common ancestor would not appreciably affect the
ensuing interpretation.

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G. Direct Selection

Since culture, generally reinforced by idiosyncratic experience, teaches the individual to regard weakness as a negative, undesirable trait, it is difficult to conceive of it as potentially advantageous. But it seems likely to the writer that man's reduction in strength maxima under non-emergency conditions has been effected historically not as an indirect result of otherwise advantageous trends in biological and cultural evolution, such as increased mutation pressure, reduced maintenance selection, or neoteny would entail, but that the reduction has been significantly advantageous throughout its development.

An advantageous characteristic may be disadvantageous if its presence reduces the development of another useful feature of greater significance. Many of the traits listed by Cureton (1947, pp. 52-53) as the "six fundamental aspects" of good physical condition -- balance, flexibility, agility, strength, power, and endurance -- conflict with one another for maximum development. Thus, regardless of exceptions to general contrasts between red and white muscle, it seems clear that certain muscles (in general, the redder ones) are better adapted for maintained aerobic operation, while others can better supply short but intensive bursts of energy, with more glycogen storage and (despite the conceptual limitations noted above) perhaps greater lactic acid "tolerance" (Ritchie, 1928, p. 39). In such a choice of emphases, man's body, it has been suggested, has found it advantageous to be constructed for speed, not strength, or perhaps for dexterity instead of strength (Riesen and Kinder, 1952, p. 17).

Especially with the development of migratory hunting of large game and the apparently nearly exclusive dependence upon hunting almost universally for the subsequent several hundred thousand years, man has been forced to adapt to long intervals without food. Furthermore, under almost all human economies in all environments, the limitation on human population has with relatively brief exceptions been that of available food resources -- apparently in contrast to chimpanzee populations, at least at the present time. So a predominant theme in human evolution has long been that of adaptation to limited and, in most economies, irregular sources of food. Such adaptations have included lowered metabolism and steatopygia, and it seems likely that another adaptation has been a general inhibition in use of near-maximal force, except under emergency.

An additional factor has been the extreme reduction in the hominid family since it arose by descent from the trees in the frequency with which near-maximal strength is needed. Migratory hunters of large mammals may require a sudden burst of energy once a day, and plant food collectors even more rarely. In contrast, the apes, which employ arboreal or semi-arboreal locomotion and feeding, encounter frequent dangers in which great strength is crucial to the avoidance of death or at least injury, as various observations of living groups and the frequency of fractured bones among arboreal apes help to attest.

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6. CONCLUSIONS

The writer would conclude that humans developed relatively weaker musculature because of two or three evolutionary factors, especially the advantage of minimized energy expenditure and also to at least some degree reduced maintenance selection.

Neither physico-chemical processes nor exercise differences -- except likely for genetically adapted differences in hypertrophic response -- account significantly for the striking superiority of chimpanzee over human strength.

Approximately a tenth of the roughly two-to-one difference per unit of body-weight in adults can be assigned to general body-size differences. Perhaps 30 per cent of the difference can be ascribed to relatively thicker muscles. Less connective tissue in the ape may add another 10 per cent, as does better leverage, likely. Non-parallelism of muscle fascicles may provide almost no increase of strength for a simple flexion at the elbow, but may contribute a 10 per cent increment to shoulder movements and, when combined with muscle length, 15 per cent for flexion at the wrist, so the effect on the scores procured by the writer will be estimated at 5 per cent. Slightly greater glycogen reserves and tolerance to lactic acid seem moderately likely for the chimpanzee, but would in any case probably not have an appreciable effect even during strength tests of moderate duration. Greater capillary density seems probable in the chimpanzee, but this would likely be associated with little alteration in strength scores and should even result in some decreases for very brief tests. However, capillary development likely accounts in large part for the marked contrasts in great endurance in chimpanzees versus little endurance in humans manifested in the subjects compared (Edwards, 1965g). Finally, the writer considers that, in response to different selective optima, the chimpanzee manifests much greater ease and frequency of motor unit innervation, likely amounting to a 25 per cent superiority. This estimate is made despite the observational evidence for manifestations of strength markedly above these maxima under conditions of extreme fear or rage (Edwards, 1963f); tending to adjust the estimated percentage in the opposite direction is the remarkably low variability of the chimpanzee strength scores recorded by the writer (1965g), which seems to suggest an approach to the 100 per cent limiting asymptote, as in champion weightlifters (1963a).

The perhaps somewhat striking conclusion of the writer is that not one or two but apparently at least five or six separate factors significantly affect the marked differences in chimpanzee and human strength scores. Although the apparently quite moderate estimates made of the proportionate differences in these factors total only 90 per cent additively, the product of the separate ratios is 2.25, which seems to suggest slight overestimates for a couple of the factors; but the actual ratio of chimpanzee superiority to man in strength per unit of body-weight may exceed 2.25, as will be calculated more precisely in the final paper in this series (Edwards, 1965g).

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13 ABSTRACT

Detailed consideration and testing of hypotheses against available data indicate that the marked two-to-one superiority of chimpanzee over human upper extremity strength per unit of body-weight is apparently due to a combination in the chimpanzee of relatively larger upper extremities, higher proportions of contractile material, smaller average body-size, muscle origins and insertions farther from joints, obliquity of muscle fibers, greater capillary density and glycogen storage in muscles, and greater frequency and ease of innervating a higher percentage of motor end-plates, but not so different physico-chemical processes of muscular contraction and not, among the subjects tested, significantly to difference in exercise, although somewhat differential response to equivalent exercise is likely.

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